SIMULATED SEASONAL AND INTERANNUAL VARIABILITY IN LARVAL TRANSPORT AND OCEANOGRAPHY IN THE NORTHWESTERN HAWAIIAN ISLANDS USING SATELLITE REMOTELY SENSED DATA AND COMPUTER MODELING

BY

DONALD R. KOBAYASHI[1] and JEFFREY J. POLOVINA[1]

ABSTRACT

Larval transport and oceanographic conditions experienced by pelagic larvae in the Northwestern Hawaiian Islands were simulated using an individual-based approach to track daily movements in a Lagrangian modeling framework. These advection-diffusion models were configured with 1°x1° resolution, monthly geostrophic currents estimated from satellite altimetry. Larval dispersal was simulated for each month of the year from 1993-2002 for 3-, 6-, and 12-month larval durations. Four release locations were evaluated: Midway Island, Maro Reef, Necker Island, and Oahu. Larval retention was evaluated by tabulating successfully simulated settlement, which was scored based on larval proximity to release sites after completion of the pelagic duration. Sea surface temperature and chlorophyll concentration at each daily larval location were tabulated utilizing similar resolution, satellite remotely sensed data products (NOAA Pathfinder AVHRR SST and SeaWiFS ocean color), and these *in situ* values were integrated over the entire larval duration for each larval track. These oceanographic variables are of critical importance in the early life history because of their hypothesized relationships to larval growth and feeding success, both critical determinants of larval survival and successful recruitment. The sea surface temperature and chlorophyll histories experienced by successfully settling larvae display strong seasonal and interannual patterns, which were decomposed using generalized additive models (GAMs). These patterns may be useful towards understanding episodic recruitment events, as well as for posing hypotheses towards understanding the mechanisms underlying spawning seasonality. These transport dynamics and oceanographic patterns have general implications for a variety of vertebrate and invertebrate metapopulations in the Northwestern Hawaiian Islands and their effective management.

[1]NOAA Pacific Islands Fisheries Science Center, 2570 Dole Street, Honolulu, HI 96822 USA,
E-mail:Donald.Kobayashi@noaa.gov

INTRODUCTION

Temporal patterns of reproduction are a widespread phenomenon in both plant and animal ecology. Organisms can maximize their fitness by propagating at times which are optimal for maximum reproductive output and/or enhanced survival of their young. It is commonly thought that the latter is of more importance for highly fecund aquatic species which broadcast their abundant young into the pelagic environment (Johannes, 1978; Thresher, 1984). Several scales of temporal variability may be of importance in the timing of reproduction. Diel patterns, such as spawning near dawn or dusk, may be important to minimize predation on both the spawning individuals and their pelagic propagules (e.g., Doherty, 1983). Lunar patterns, such as spawning near spring tides (full and new moon) may be related to key variables which change consistently on a monthly scale such as tidal currents and moonlight illumination (e.g., May et al., 1979). Seasonal patterns, such as spring or summer spawning, may be related to key variables which change consistently on an annual scale such as currents, plankton blooms, and temperature (Johannes, 1981). Seasonality in spawning has been well documented in a variety of Hawaiian fish and invertebrate species (e.g., Itano, 2000; Lobel, 1989; Randall, 1961; Reese, 1968; Walsh, 1987). Various hypotheses have been put forth to explain such seasonality. Johannes (1978) has argued that predatory losses on pelagic propagules have been a driving selective force for spawning seasonality. More recent views of pelagic larval transport have emphasized the importance of retention with the view that many marine populations are more closed than open (Cowen, 2002; Cowen et al., 2003; Jones et al., 1999; Kingsford et al., 2002; Leis, 2002; Mora and Sale, 2002; Robertson, 2001; Sponaugle et al., 2002; Swearer et al., 1999). While predation and retention issues may be important, the predominately oligotrophic pelagic environment has led some to suggest that larval food supply is the single most important factor governing the numbers of marine fish (Cushing, 1972). Reese (1968) suggested that the different spawning seasons used by ecologically similar species of hermit crabs were a mechanism to reduce competition for pelagic larval food, and that there would be selective advantage to offsetting reproductive periods if larval food supply were a limiting factor. Larval food supply involves spatial and temporal patchiness, and the species composition of the phytoplankton and microzooplankton is critically important (Lasker, 1975). In addition to starvation issues, variability in food supply has been shown to be an important determinant of larval growth and subsequent survival (e.g., Booth and Alquezar, 2002). Faster growth has been hypothesized to favor survival by reducing cumulative predatory mortality (e.g., Anderson, 1988). Leis and Carson-Ewart (1999) suggest that larger size is an important factor for evading predation during the settlement process, citing fin erection behavior and importance of speed when fleeing predators, based on field experiments with coral trout larvae. It is possible that small size may be an advantage for remaining undetected during settlement; however, the advantages of being larger in the plankton probably outweigh the disadvantages, considering the gauntlet of size-based pelagic predators (reviewed by Purcell and Arai, 2001; Zaret, 1980). Additionally, larvae which grow faster may retain a size and survivorship advantage during the critical first few weeks post-settlement on the reef (Bergenius et al., 2002; Booth and Hixon

1999; Sponaugle and Pinkard, 2004). While size is most directly a function of age, both food and ambient temperature have been shown to have a strong positive effect on larval growth (e.g., Buckley et al., 2004). Clearly, in addition to physical retention, there is a suite of other considerations critical in the early life history survival of insular species. These important ecological considerations can be synthesized within a computer simulation using available tools and data products.

Earlier works have used advection-diffusion models to examine larval transport and retention (e.g., Griffin et al., 2001; Hill, 1991; Polovina et al., 1999; Siegel et al., 2003). Few such applications have integrated the oceanographic conditions experienced by individual larvae directly into the model. With the availability of remotely sensed data products, it is logical to incorporate these environmental fields into the computer simulation framework, particularly with individual-based modeling approaches (e.g., Mullon et al., 2002). Sea surface temperature (SST) and chlorophyll-a concentration are widely available from a variety of satellite sensors, and both of these variables may have important linkages to the ecology of early life history stages, as described above for growth and mortality. The goals of this paper are to examine, via computer simulation and use of remotely sensed environmental data, the seasonal and interannual components of larval retention, transport, growth, and survival in selected regions of the Hawaiian Archipelago.

MATERIALS AND METHODS

Simulated larval releases were stratified by year (n=10: 1993-2002), month (n=12: January-December), locations spanning the Hawaiian Archipelago (n=4: Midway, Maro, Necker, and Oahu, see Fig. 1), and larval duration (n=3: 3, 6, and 12 months) to yield a total of 1,440 model treatments. These larval durations were chosen to bracket the known durations of several commercially important species of lobster and deep-water bottomfish. Five thousand simulated larvae were released for each model treatment for a total of 7.2 million individuals. Each individual was tracked daily for the entire larval duration in Lagrangian fashion using the following equations:

$$x_{t+\Delta t} = x_t + \left[u_{(x_t,y_t,t)}\Delta t + \varepsilon\sqrt{D\Delta t} \right] / \cos(y_t)$$
$$y_{t+\Delta t} = y_t + \left[v_{(x_t,y_t,t)}\Delta t + \varepsilon\sqrt{D\Delta t} \right]$$

where x represents longitude, y represents latitude, t represents time in days, u represents the East/West component of the current speed, v represents the North/South component

of the current speed, $\cos(y_t)$ adjusts distance by latitude to account for the spherical coordinate system, and D is the diffusivity coefficient (500 m^2/sec following Polovina et al., 1999). The currents utilized in this study were monthly 1° latitude/longitude resolution geostrophic flow fields calculated from satellite altimetry obtained from CNES/AVISO/SSALTO (CLS Space Oceanography Division, France). Integrated SST and chlorophyll-a histories encountered daily by individual larvae were tabulated daily

using interpolations from monthly 1° latitude/longitude resolution data grids. SST data were obtained from the MCSST (NOAA Pathfinder AVHRR satellites) product from NASA/JPL. Chlorophyll-a data was obtained from the Sea-viewing Wide Field-of-View Sensor (SeaWiFS) instrument on board the Seastar satellite. Integration was performed by averaging the daily SST or chlorophyll-a interpolations over the entire pelagic duration. Additionally, only averages from the subset of larvae scored as successfully being retained by the source site following completion of the entire pelagic duration were tabulated to each treatment. A 140-km radius for scoring larval retention was used, similar to Polovina et al. (1999). This is an arbitrary threshold utilized as a compromise to achieve some larval settlement at this level of propagule sample size (n=5,000). Since settlement success was evaluated in a relative manner (e.g., comparing between years, months, sites, pelagic durations), this exact dimension is not critical. For each of the 1,440 treatments, the following were tabulated: the number of larvae scored as retained, the number of larvae scored as settling at Oahu, the number of larvae scored as not settling at any of the four sites, the average SST encountered by this subset of retained larvae, and the average chlorophyll-a encountered by this subset of retained larvae. SST was available for the entire temporal duration of this analysis; however, chlorophyll-a data were available only from 1997 onwards. The advection-diffusion model was written in the open-source software XBASIC (http://www.xbasic.org) and run on an Intel P4 Windows XP system. Generalized Additive Models (GAMs) were used to identify relationships between a suite of response variables (retention, SST history, or chlorophyll-a history) and a suite of predictor variables (year, month, location, and pelagic duration). GAM is a relatively new analytical technique (Hastie and Tibshirani, 1990) which is useful when the predictor variables have unknown *a priori* and possibly nonlinear effects upon the response variable. GAM analysis was carried out using the analytical software package S-Plus v. 6.1.2r2 on an Intel P4 workstation using Redhat LINUX 7.3 OS. Six GAM analyses were performed as outlined in Table 1, with each utilizing a different suite of predictor variables as described. The graphical output in the form of smoothing splines and comparative categorical effects serve as the primary basis for interpretation, using standard error terms to indicate statistical significance. The GAM plots indicate the modeled relationships between the suite of predictor variables and the response variable, and the cumulative (hence additive) sum across each predictor function scaled by an intercept results in the predicted value for the response variable. Higher values along the y-axis indicate a higher contribution towards the predicted value for the response variable, and vice-versa.

RESULTS

Retention varied from a low of 0/5,000 (scored for 39 different treatments) to a high of 3,908/5,000 (scored for October, 1993, Midway, 3-month release). Retention was strongly related to year and larval duration, and had weak relationships to month and site (Figs. 2A-2D). Larval settlement at Oahu was strongly dependent on spawning site (Fig. 3). The Oahu settlement GAMs were run separately for the spatial effect and other

variables due to the numerous zeros in the data for sites farther from Oahu. For example, 85% of the Midway runs yielded 0 larval settlement to Oahu, and the small amount of successful settlement was accomplished only at the longest larval duration (Table 2). This lack of data contrast in other sites effectively weighted the GAM primarily towards the Oahu site, leading to difficult interpretation. Hence, the GAM was run separately for each site (Figs. 4-7), with the last GAM being a simple retention analysis for Oahu only. Strong yearly effects were observed in all sites, with weak monthly effects, and duration only becoming important at Necker and Oahu. Oahu settlement was favored by a longer larval duration from Necker (Fig. 6C, the closest site to Oahu), and by a shorter larval duration from Oahu itself (Fig. 7C).

Larval nonsettlement was cursorily examined in this analysis. Considering that there are abundant other sites available for larval settlement, this result should be treated with caution. However, by examining the larvae that did not settle at any of the four sites, some useful hypotheses can be posed for further analyses. The data suggest that yearly and monthly effects may be relatively weak and that perhaps there is a spatial component involved with Oahu exhibiting higher rates of larval loss (Fig. 8C). As expected, a longer larval duration is positively correlated to larval non-settlement (Fig. 8D).

SST and chlorophyll-a histories had strong yearly, monthly, and site relationships (Figs. 9-14), with the expected deterioration of a seasonal effect at a 12-month larval duration (Figs. 11B, 14B). For a 3-month larval duration, SST history was optimized by a July-August spawning, peaking in late July/early August (Fig. 9B). For a 6-month larval duration, the optimal spawning with respect to SST history is offset accordingly to May-July, peaking in June (Fig. 10B).

DISCUSSION

Larval retention and loss were found to depend primarily on larval duration. The negative relationship between retention and larval duration is intuitive, in that a longer larval duration implies a greater chance of long-distance transport with subsequent loss to the system. This is similar to the findings of Leis and Miller (1976), who found that larvae of demersal-spawning reef fish (shorter pelagic duration) tended to be found closer to shore than larvae from pelagic-spawning reef fishes (longer pelagic duration). Some of the proposed physical mechanisms which can transport reef fish larvae back to their spawning site operate on the time scale of 2-3 months (e.g., Lobel and Robinson, 1986), consistent with the relatively high retention found in this study for a 3-month larval duration. Late-stage larvae of some reef fishes can occur at great distances from suitable adult habitat (e.g., Clarke, 1995; Victor, 1987), but are of unknown importance for local population persistence. This issue of long-distance dispersal may, however, be important for larval interchange in a metapopulation framework, which will be examined elsewhere for insular species in the Hawaiian Archipelago (Kobayashi, in preparation). The interannual pattern of retention (Fig. 2A) is consistent with observed large-scale changes in the central Pacific Ocean (e.g., Polovina et al., 1994); however, the exact mechanism remains unknown at this point. Larval settlement at Oahu examined by source

also appeared to be a proximity effect, with settlement negatively correlated with distance from Oahu. Larval duration was an important effect when examining Oahu settlement from the adjacent site at Necker (Fig. 6C); however, even at the longest durations, the numbers reaching Oahu from Necker did not surpass the number being retained around Oahu from Oahu on average (Table 2). Additional modeling is underway to better understand connectivity in the Archipelago and will address this on a finer spatial resolution, both in terms of source/sink dynamics and oceanographic input data.

There appears to be an interesting tradeoff between SST and chlorophyll-a with respect to seasonal spawning (Figs. 9B, 10B, 12B, 13B). Summer spawning is clearly conducive to placing the larvae into higher SST water masses; however, winter spawning clearly maximizes chlorophyll-a experienced by larvae. This dilemma does not appear to be mediated by seasonal retention (Fig. 2B) or seasonal nonsettlement (Fig. 8B). Early summer and late summer may be satisfactory compromises to best optimize these factors, thereby keeping both SST and chlorophyll-a at relatively high levels during the pelagic stages. The four spawning sites examined in this study generally fall along a latitudinal transect, and the resulting site-related patterns in SST and chlorophyll-a are consistent with oceanographic work in this area (Polovina et al., 2001; Seki et al., 2002). The lowest SST and highest chlorophyll-a occur at the northernmost release site of Midway, which is well within the TZCF (Transition Zone Chlorophyll Front). At lower latitudes, there is a trend for higher SST values, as well as higher chlorophyll-a values. The latter may be due to increased nearshore processes (e.g., island effects) enhancing productivity around the larger islands in the Archipelago (e.g., Seki et al., 2001).

In summary, it has been shown that computer simulation may be a useful approach towards understanding important aspects of early life history and adult spawning ecology. Retention, transport, and environmental variables are shown to be expressed in complex spatial and temporal patterns. The utility of this approach depends critically on the passivity of larvae. Some late-stage fish larvae have been shown to be capable of directional orientation and active movement near the timing of settlement (e.g., Kingsford et al., 2002; Leis and Carson-Ewart, 1999; 2000; 2002; 2003; Leis et al., 2003; Tolimieri et al., 2004; Jeffs et al., 2003); however, it is quite likely that early life history stages (eggs and early-stage larvae) are passive drifters for a large part of the pelagic duration, and lobster phyllosoma have very limited swimming abilities. The findings of this simulation study can be used to pose further hypotheses and corroborate existing empirical evidence. In the latter case, for example, there are observed biogeographic patterns in the Hawaiian Archipelago which would benefit from a more quantitative mechanistic explanation, such as a higher rate of endemism being found at the northerly atolls (DeMartini and Friedlander, 2004), the faunal similarity between Johnston Atoll and the Main Hawaiian Islands (Kosaki et al, 1991), and the pattern of spread of introduced/invasive species such as the blue-lined snapper *Lutjanus kasmira* (Friedlander et al., 2002). Such corroboration could serve as potential ground-truthing for the modeling approach. Additionally, the SST and chlorophyll-a histories provide a useful environmental perspective to recent findings emphasizing the importance of larval physiological fitness (e.g., Berkeley et al., 2004) towards population maintenance. Incorporating demographic variability into the transport-modeling framework is a

logical next step. The modeling efforts as described here can help understand and predict recruitment success, when coupled with empirical observations and field experiments. A better understanding of oceanographic source-sink dynamics and connectivity throughout the Archipelago will be helpful towards design of marine protected areas (MPAs) and reserves (Cowen, 2002), and will contribute towards more effective management and resource utilization in the NWHI.

ACKNOWLEDGEMENTS

Table 1. Summary of GAM analyses.

Response variable	Predictor variable(s)
Larval retention (all data)	Year, Month, Site, and Duration
Larval settlement at Oahu (all data)	Site
Larval settlement at Oahu (separately by site)	Year, Month, and Duration
Larval non-settlement (all data)	Year, Month, Site, and Duration
Integrated SST history of retained larvae (separately by duration)	Year, Month, and Site
Integrated chlorophyll-a history of retained larvae (separately by duration)	Year, Month, and Site

Table 2. Summary of larval settlement at Oahu, aggregated by year and month, from different spawning sites and for different larval durations. The average number reaching Oahu is out of 5,000 releases; the number of combinations with zero is out of 120 different year and month combinations per site/duration strata.

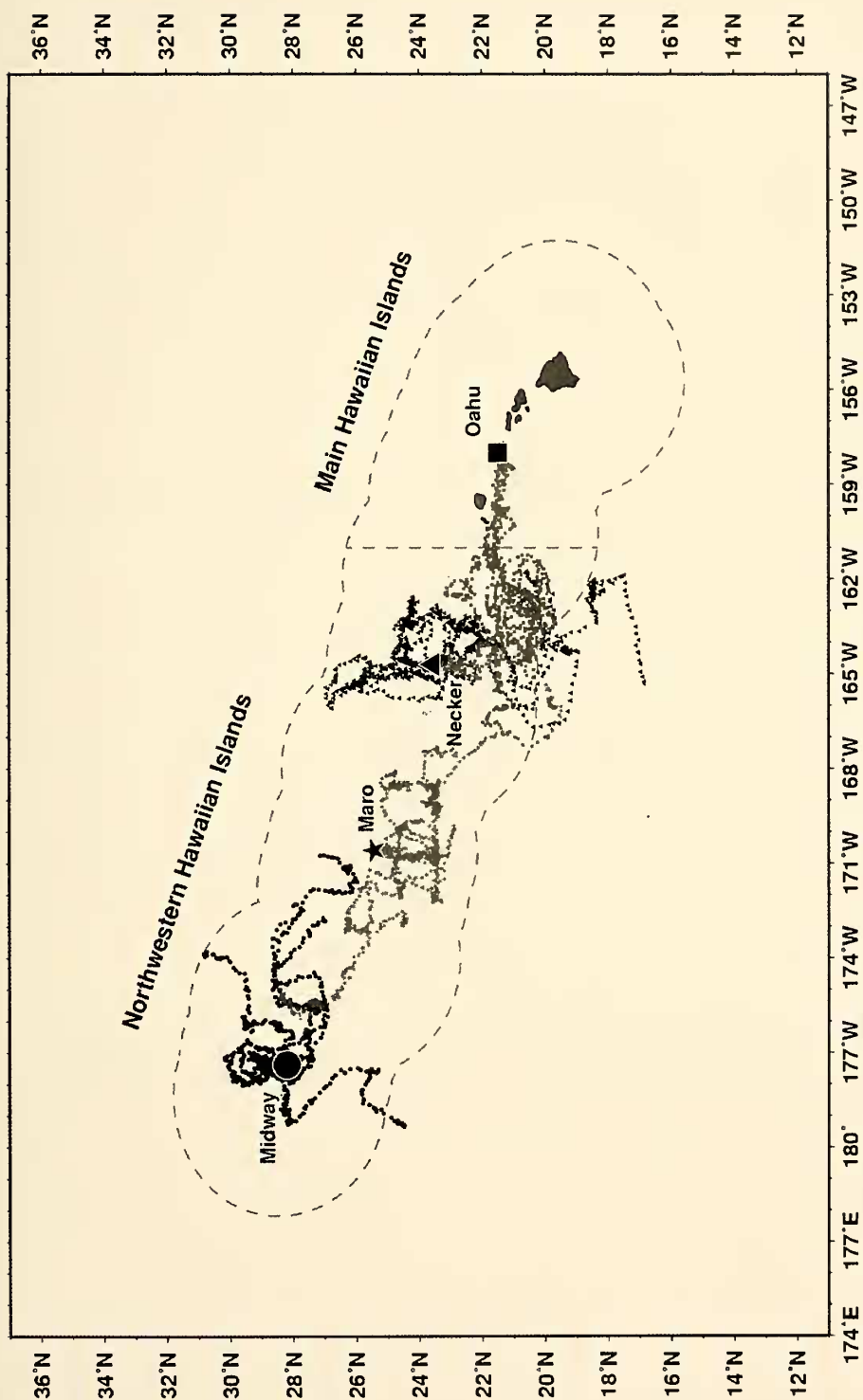| Site	Duration	Average no. reaching Oahu	No. combinations with zero
Midway	3-month	0.00	120
	6-month	0.00	120
	12-month	5.10	66
Maro	3-month	0.00	120
	6-month	14.61	93
	12-month	45.15	14
Necker	3-month	55.61	82
	6-month	85.52	29
	12-month	98.12	0
Oahu	3-month	732.73	8
	6-month	297.02	2
	12-month	126.47	0

373

Figure 1. Map of Hawaiian Archipelago indicating larval release sites used in this analysis. Five sample releases from each site for a 6-month pelagic duration are shown for illustrative purposes only.
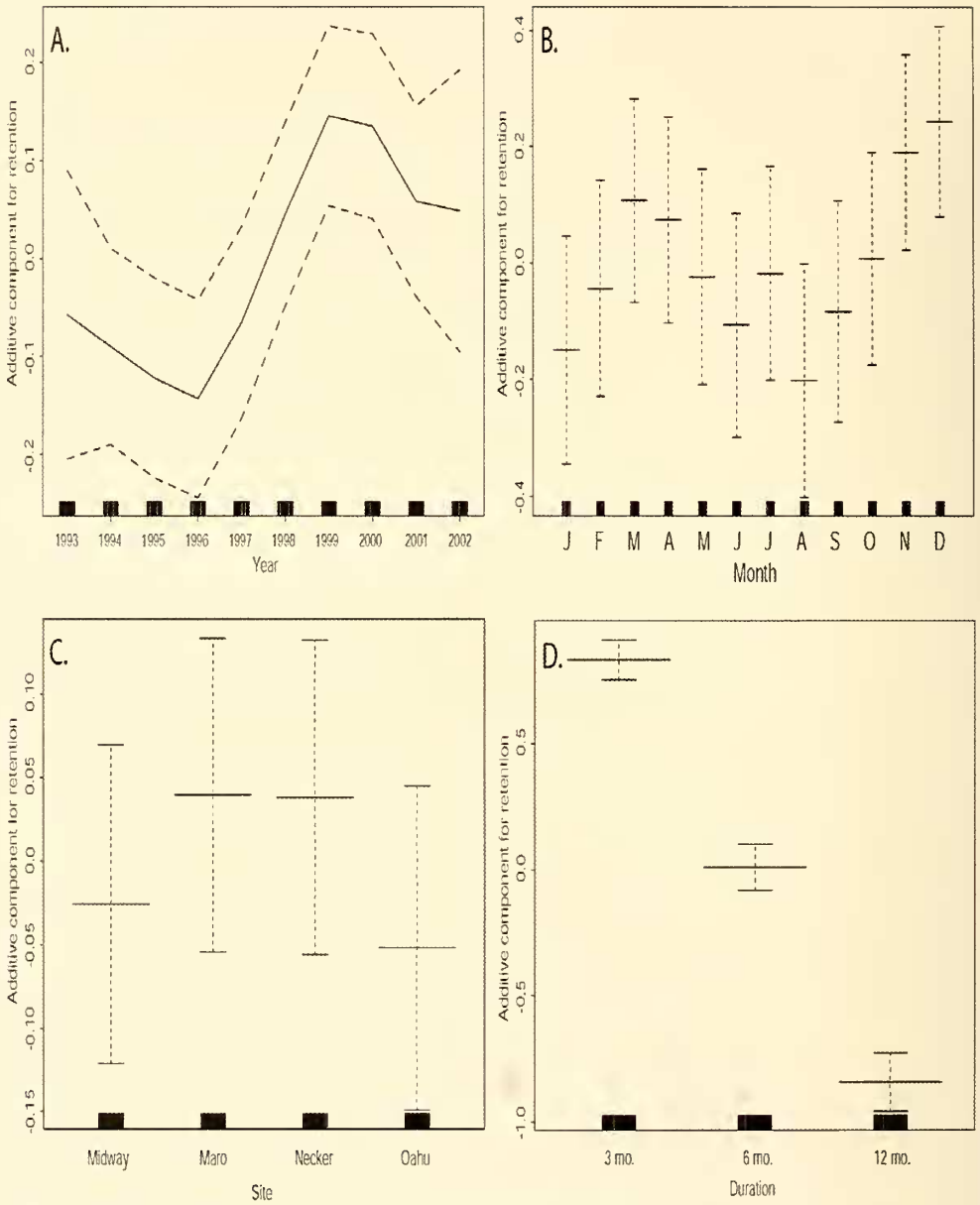
Figure 2. Results of GAM application to larval retention. The predictor variables are year (A), month (B), spawning site (C), and larval duration (D). C.I. are ±2 standard errors.
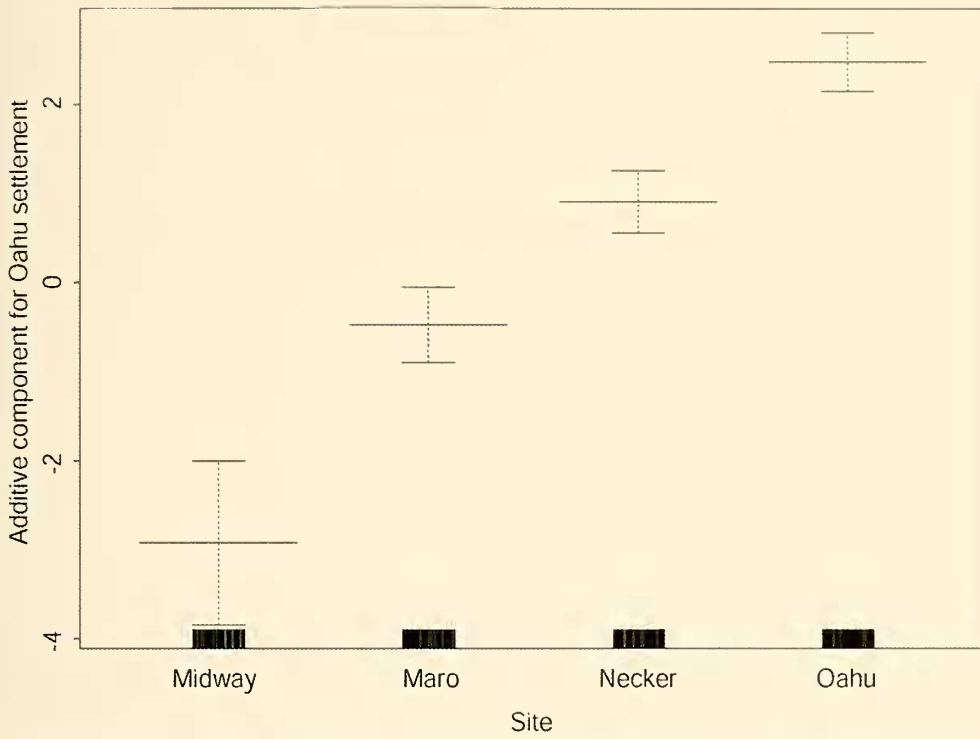
Figure 3. Results of GAM application to larval settlement at Oahu. The predictor variable is spawning site. C.I. are ±2 standard errors.
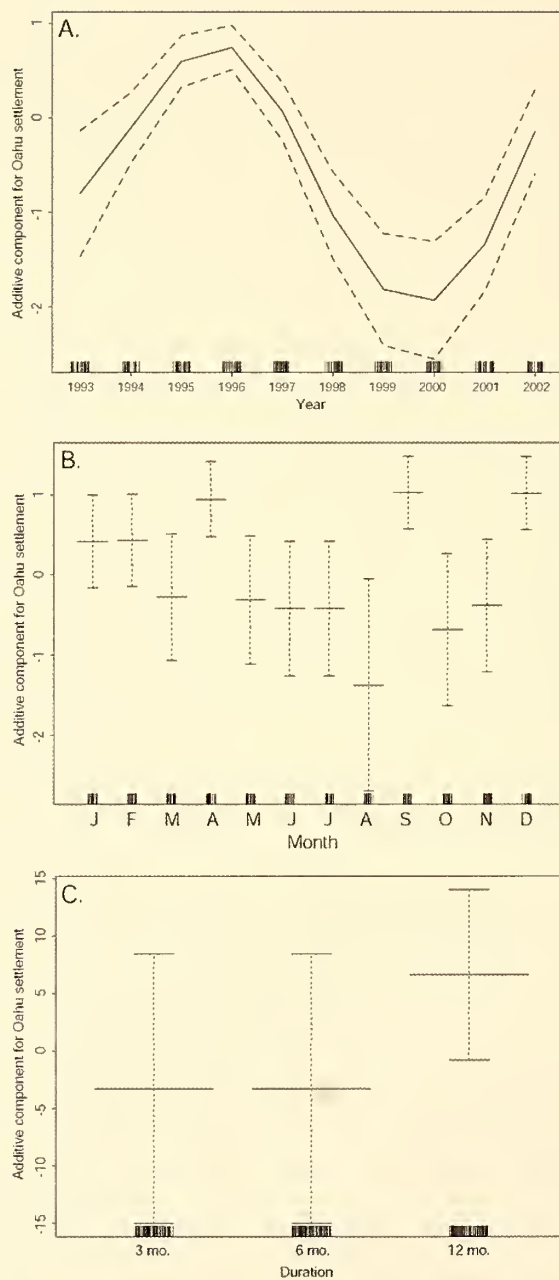
Figure 4. Results of GAM application to larval settlement at Oahu from Midway spawning. The predictor variables are year (A), month (B), and larval duration (C). C.I. are ±2 standard errors.
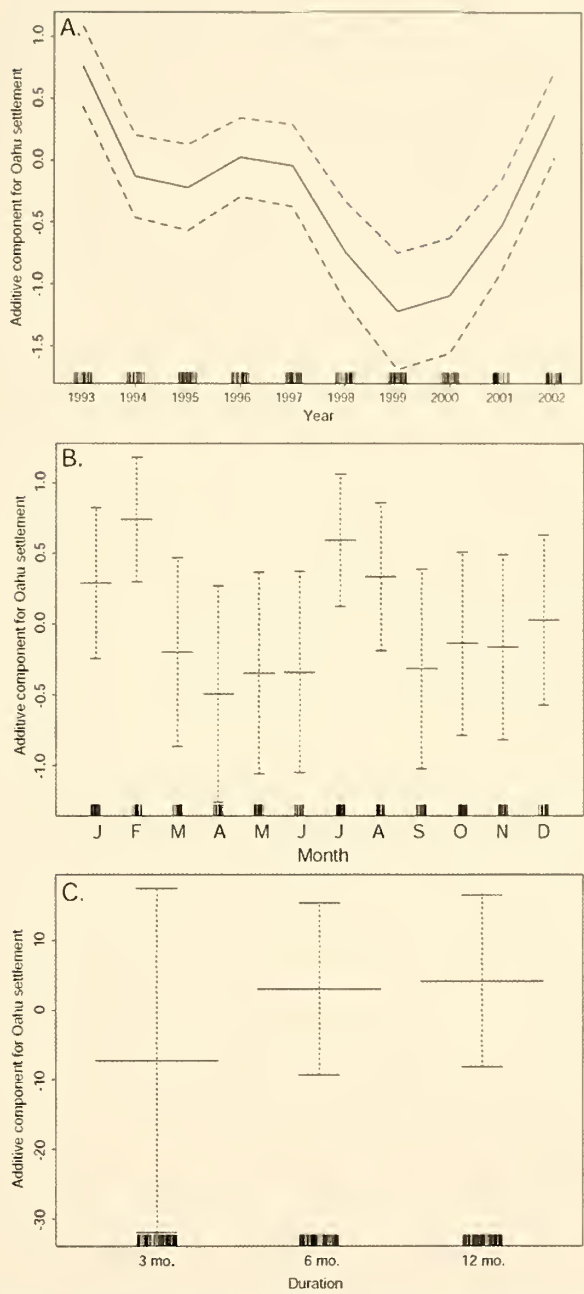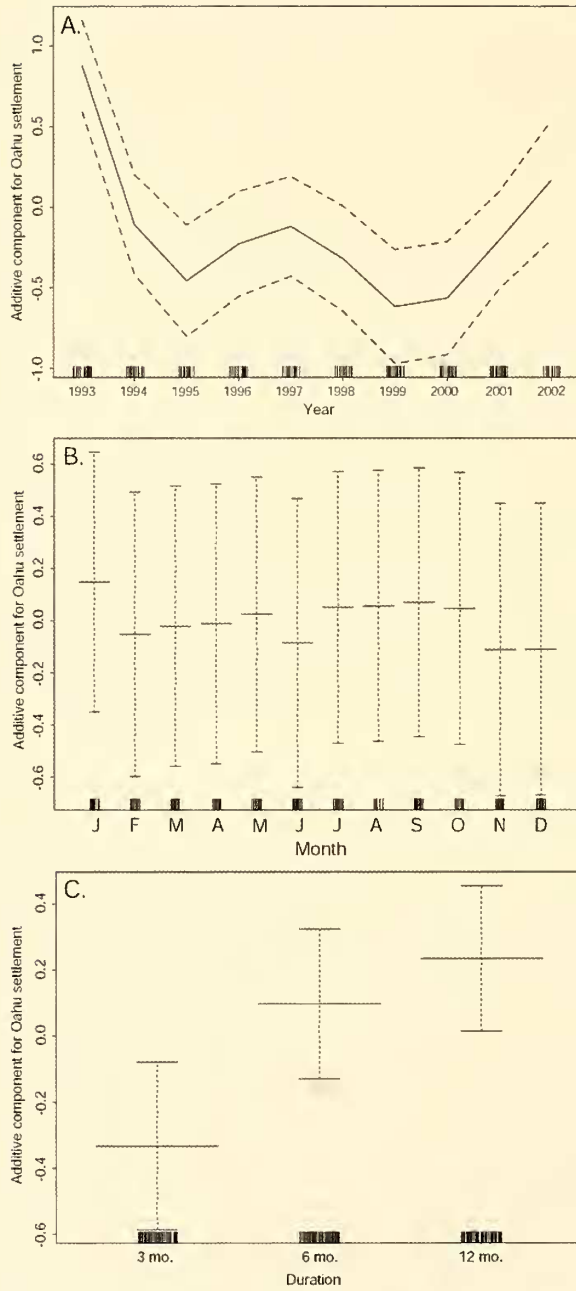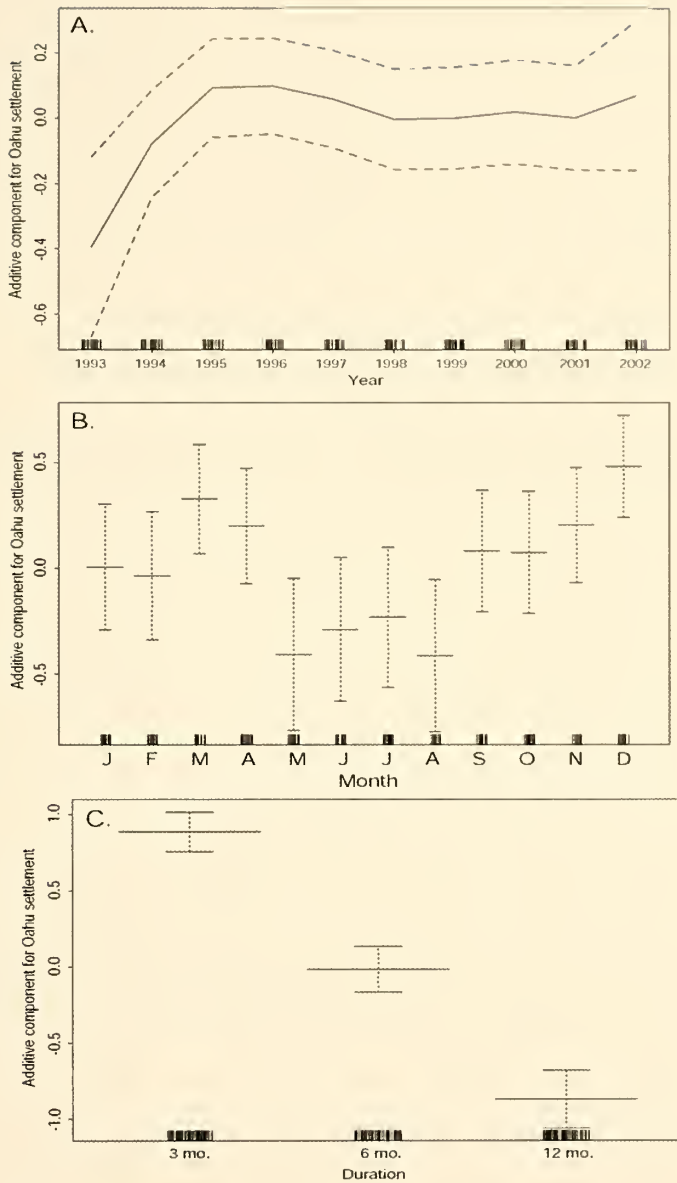
Figure 5. Results of GAM application to larval settlement at Oahu from Maro spawning. The predictor variables are year (A), month (B), and larval duration (C). C.I. are ±2 standard errors.

Figure 6. Results of GAM application to larval settlement at Oahu from Necker spawning. The predictor variables are year (A), month (B), and larval duration (C). C.I. are ±2 standard errors.

Figure 7. Results of GAM application to larval settlement at Oahu from Oahu spawning. The predictor variables are year (A), month (B), and larval duration (C). C.I. are ±2 standard errors.
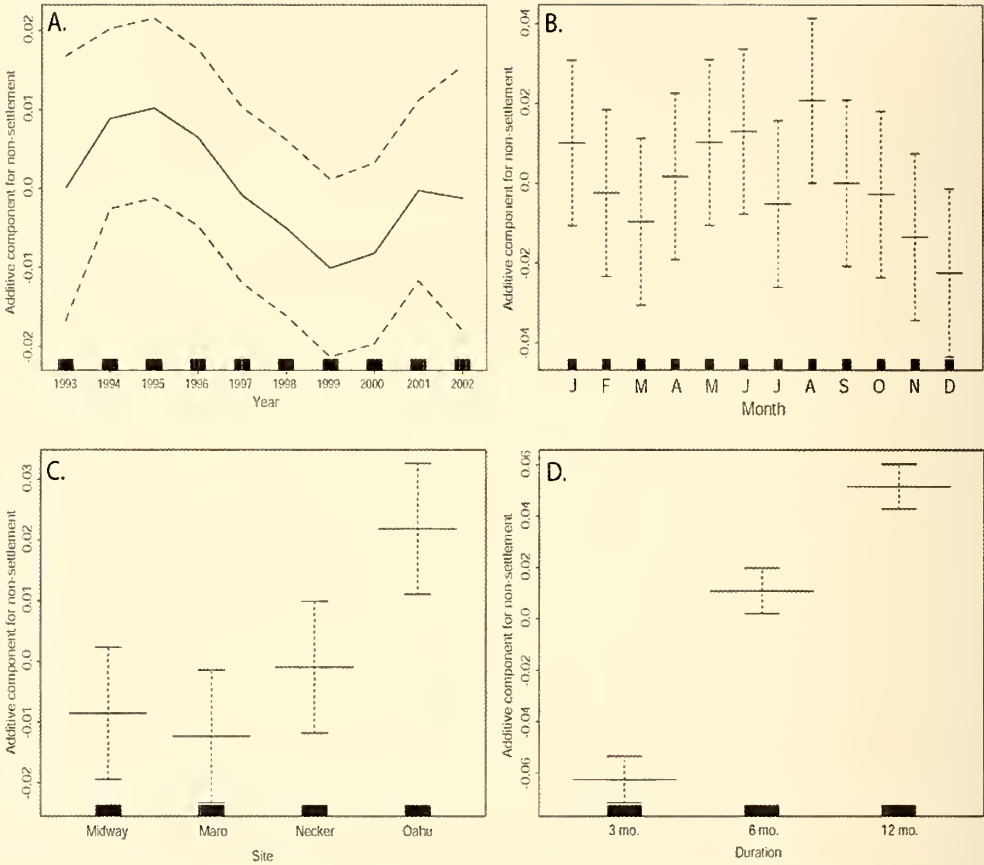
Figure 8. Results of GAM application to larval nonsettlement. The predictor variables are year (A), month (B), spawning site (C), and larval duration (D). C.I. are ±2 standard errors.
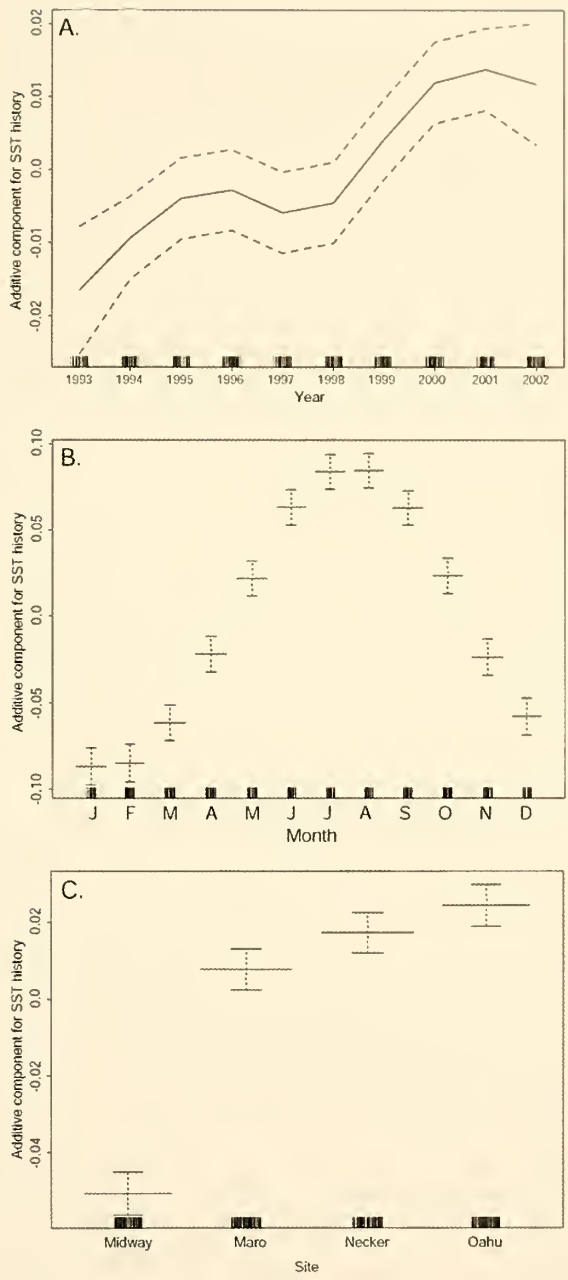
Figure 9. Results of GAM application to SST history of retained larvae after 3-month pelagic duration. The predictor variables are year (A), month (B), and spawning site (C). C.I. are ±2 standard errors.

Figure 10. Results of GAM application to SST history of retained larvae after 6-month pelagic duration. The predictor variables are year (A), month (B), and spawning site (C). C.I. are ±2 standard errors.
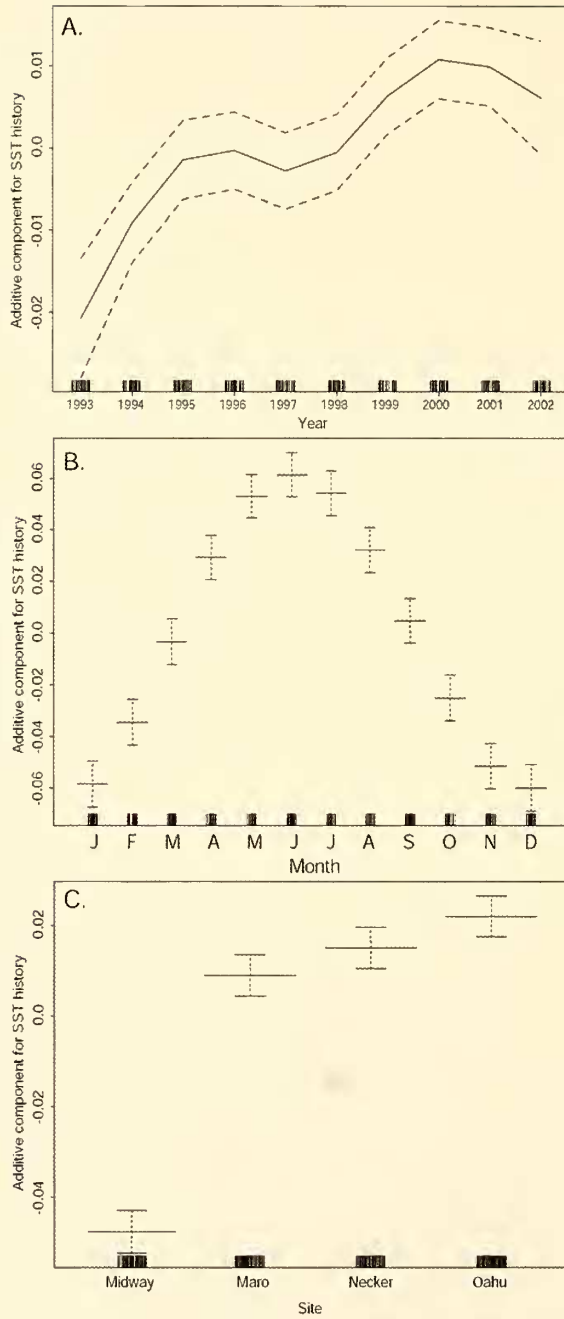
383

Figure 11. Results of GAM application to SST history of retained larvae after 12-month pelagic duration. The predictor variables are year (A), month (B), and spawning site (C). C.I. are ±2 standard errors.

Figure 12. Results of GAM application to chlorophyll-a history of retained larvae after 3-month pelagic duration. The predictor variables are year (A), month (B), and spawning site (C). C.I. are ±2 standard errors.
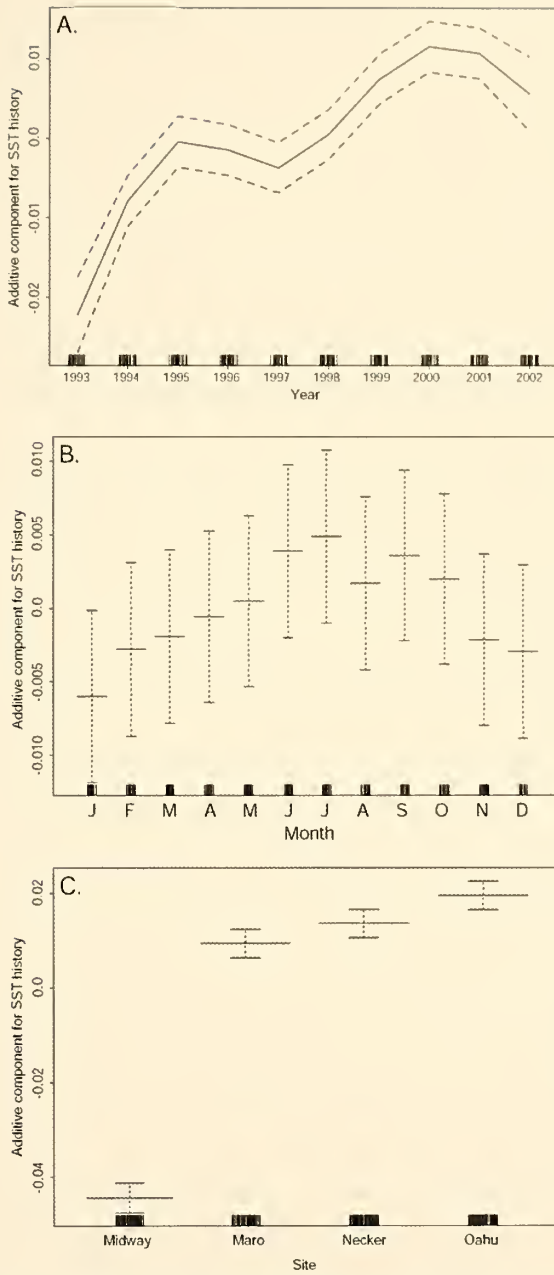
Figure 13. Results of GAM application to chlorophyll-a history of retained larvae after 6-month pelagic duration. The predictor variables are year (A), month (B), and spawning site (C). C.I. are ±2 standard errors.
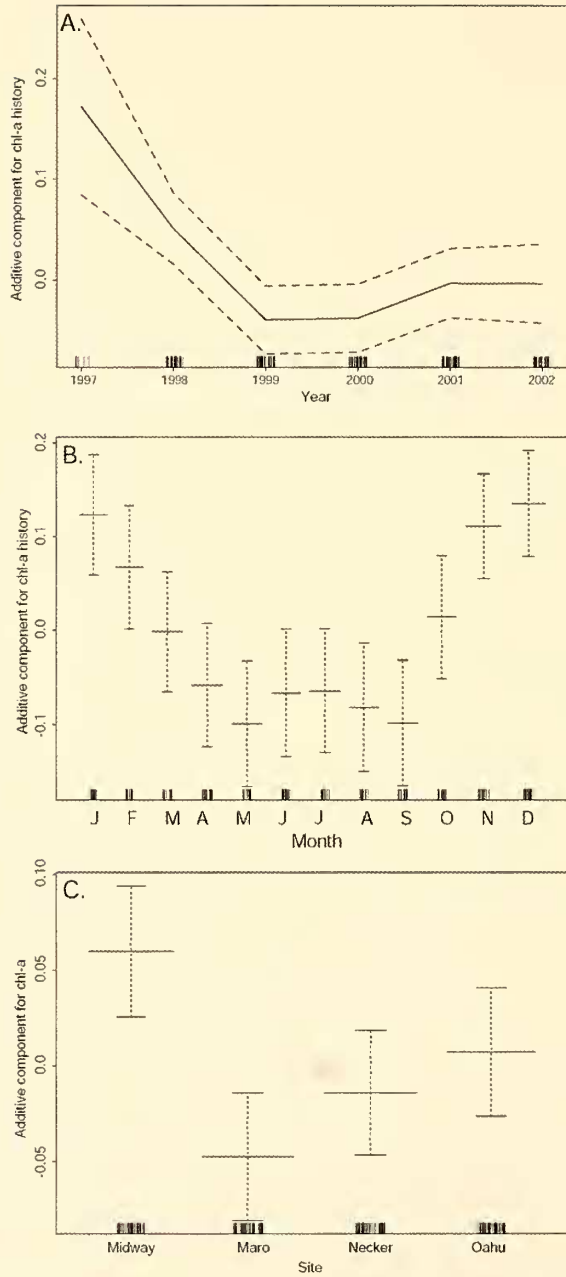
386

Figure 14. Results of GAM application to chlorophyll-a history of retained larvae after 12-month pelagic duration. The predictor variables are year (A), month (B), and spawning site (C). C.I. are ±2 standard errors.
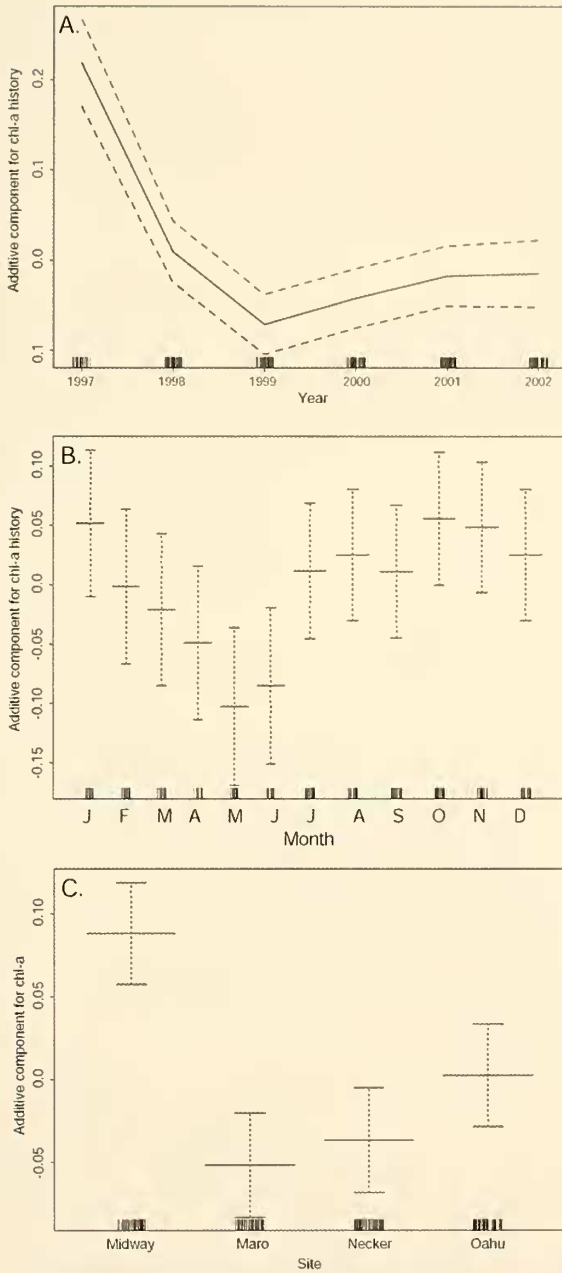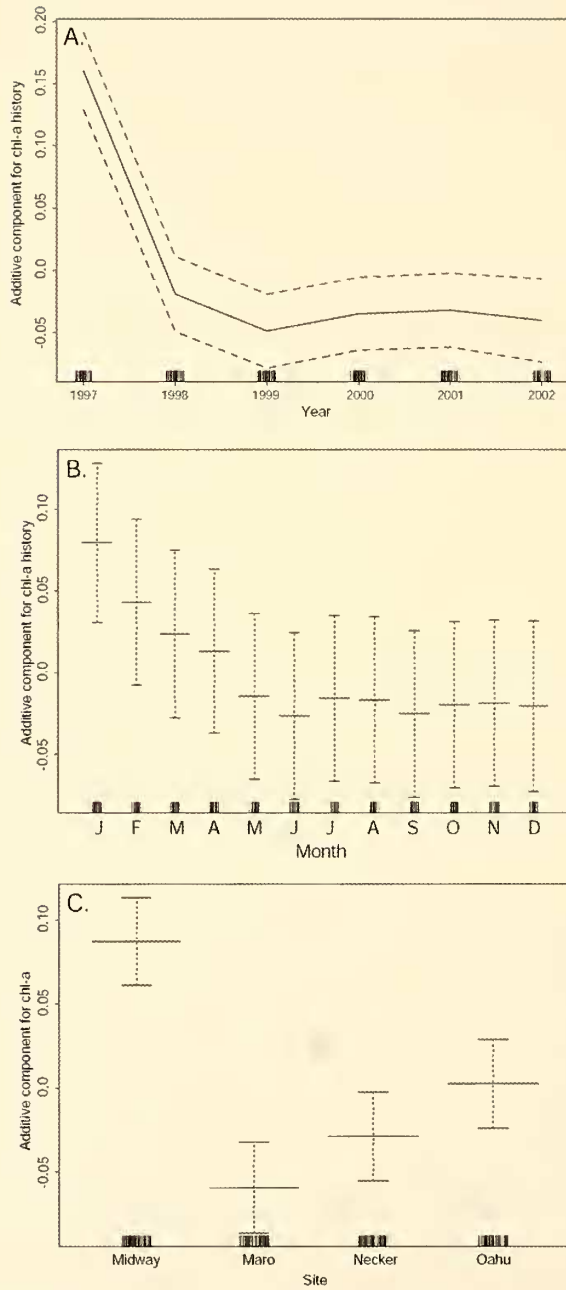
LITERATURE CITED

Anderson, J.T.
  1988. A review of size dependent survival during pre-recruit stages of fishes in relation to recruitment. *Journal of Northwest Atlantic Fishery Science* 8:55-66.
Bergenius, M.A.J., M.G. Meekan, R. Robertson, and M.I. McCormick
  2002. Larval growth predicts recruitment success of a coral reef fish. *Oecologia* 131: 521-525.
Berkeley, S.A., C. Chapman, and S.M. Sogard
  2004. Maternal age as a determinant of larval growth and survival in a marine fish, *Sebastes melanops. Ecology* 85(5):1258–1264.
Booth, D.J., and R.A. Alquezar
  2002. Food supplementation increases larval growth, condition and survival of the brooding damselfish *Acanthochromis polyacanthus* (Pomacentridae). *Journal of Fish Biology* 60:1126-1133
Booth, D.J., and M.A. Hixon
  1999. Food ration and condition affect early survival of the coral reef damselfish, *Stegastes partitus. Oecologia* 121:364-368.
Buckley, L.J., E.M. Caldarone, and R.G. Lough
  2004. Optimum temperature and food-limited growth of larval Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) on Georges Bank. *Fisheries Oceanography* 13(2):134-140.
Clarke, T.A.
  1995. Larvae of nearshore fishes in oceanic waters of the central equatorial Pacific. *Pacific Science* 49:134-142.
Cowen, R.K.
  2002. Oceanographic influences on larval dispersal and retention and their consequences for population connectivity. *Coral Reef Fishes*. Academic Press. London, New York. pp. 149-170.
Cowen, R.K., C.B. Paris, D.B. Olson, and J.L. Fortuna
  2003. The role of long distance dispersal versus local retention in replenishing marine populations. *Gulf and Caribbean Research* 14:129-137.
Cushing, D.H.
  1972. The production cycle and the numbers of marine fish. *Symposium of the Zoological Society of London* 29: 213-232.
DeMartini, E.E., and A.M. Friedlander
  2004. Spatial patterns of endemism in shallow-water reef fish populations of the Northwestern Hawaiian Islands. *Marine Ecology Progress Series* 271:281-296.
Doherty, P.J.
  1983. Diel, lunar and seasonal rhythms in the reproduction of two tropical damselfishes: *Pomacentrus flavicauda* and *P. wardi. Marine Biology* 75:215-224.
Friedlander, A.M., J.D. Parrish, and R.C. DeFelice
  2002. Ecology of the introduced snapper *Lutjanus kasmira* (Forsskal) in the reef fish assemblage of a Hawaiian bay. *Journal of Fish Biology* 60(1):28-48.

Griffin, D.A., J.L. Wilkin, C.F. Chubb, A.F. Pearce, and N. Caputi
 2001. Ocean currents and the larval phase of Australian western rock lobster, *Panulirus cygnus*. *Marine and Freshwater Research* 52:1187-1200.

Hastie, T.J., and R.J. Tibshirani
 1990. *Generalized Additive Models*. Chapman and Hall, London. 335 pp.

Hill, A.E.
 1991. Advection-diffusion-mortality solutions for investigating pelagic larval dispersal. *Marine Ecology Progress Series* 70:117-128.

Itano, D.G.
 2000. Reproductive biology of yellowfin tuna, *Thunnus albacares*, in Hawaiian waters and the western tropical Pacific Ocean: Project Summary. University of Hawaii Pelagic Fisheries Research Program Report SOEST 00-01. 75 pp.

Jeffs, A., N. Tolimieri, and J.C. Montgomery
 2003. Crabs on cue for the coast: the use of underwater sound for orientation by pelagic crab stages. *Marine and Freshwater Research* 54:841-845.

Johannes, R.E.
 1978. Reproductive strategies of coastal marine fishes in the tropics. *Environmental Biology of Fishes* 3(1):65-84.

 1981. *Words of the Lagoon: Fishing and Marine Lore in the Palau District of Micronesia*. University of California Press, Berkeley, CA, USA. 245 pp.

Jones, G.P., M.J. Milicich, M.J. Emslie, and C. Lunow
 1999. Self-recruitment in a coral reef fish population. *Nature* 402:802–4.

Kingsford, M.J., J. M. Leis, A. Shanks, K. Lindeman, S. Morgan, and J. Pineda
 2002. Sensory environments, larval abilities and local self-recruitment. *Bulletin of Marine Science* 70(1, Supplement):309-340.

Kobayashi, D.R.
 In prep. Simulated meta-population connectivity in the Hawaiian archipelago.

Kosaki, R.K., R.L. Pyle, J.R. Randall, and D.K. Irons
 1991. New records of fishes from Johnston Atoll, with notes on biogeography. *Pacific Science* 45:186-203.

Lasker, R.
 1975. Field criteria for survival of anchovy larvae: The relation between inshore chlorophyll maximum layers and successful first feeding. *Fishery Bulletin* 73(3):453-462.

Leis, J.M.
 2002. Pacific coral-reef fishes: the implications of behaviour and ecology of larvae for biodiversity and conservation, and a reassessment of the open population paradigm. E*nvironmental Biology of Fishes* 65(2):199-208.

Leis, J.M., and B.M. Carson-Ewart
 1999. In situ swimming and settlement behaviour of larvae of an Indo-Pacific coral-reef fish, the Coral Trout (Pisces, Serranidae, *Plectropomus leopardus*). *Marine Biology* 134(1):51-64.

 2000. Behaviour of pelagic larvae of four coral-reef fish species in the ocean and an atoll lagoon. *Coral Reefs* 19:247-257.

2002. *In situ* settlement behaviour of damselfish (Pomacentridae) larvae. *Journal of Fish Biology* 61:325-346.

2003. Orientation of pelagic larvae of coral-reef fishes in the ocean. *Marine Ecology Progress Series* 252:239-253.

Leis, J.M., B.M. Carson-Ewart, A.C. Hay, and D.H. Cato

2003. Coral-reef sounds enable nocturnal navigation by some reef-fish larvae in some places and at some times. *Journal of Fish Biology* 63:724-737.

Leis, J.M., and J.M. Miller

1976. Offshore distributional patterns of Hawaiian fish larvae. *Marine Biology* 36(3): 359-367.

Lobel, P.S.

1989. Ocean current variability and the spawning season of Hawaiian reef fishes. *Environmental Biology of Fishes* 24:161-171.

Lobel, P.S., and A.R. Robinson

1986. Transport and entrapment of fish larvae by ocean mesoscale eddies and currents in Hawaiian waters. *Deep-Sea Research* 33:483-500.

May, R.C., G.S. Akiyama, and M.T. Santerre

1979. Lunar spawning of the threadfin *Polydactylus sexfilis*, in Hawaii. *Fishery Bulletin* 76(4):900-904.

Mora, C., and P.F. Sale

2002. Are populations of coral reef fish open or closed? *Trends in Ecology and Evolution* 17:422-428.

Mullon C., P. Cury, and P. Penven

2002. Evolutionary individual-based model for the recruitment of the anchovy (*Engraulis capensis*) in the southern Benguela. *Canadian Journal of Fisheries and Aquatic Sciences* 59:910-922.

Polovina, J.J., E.A. Howell, D.R. Kobayashi, and M.P. Seki

2001. The transition zone chlorophyll front, a dynamic global feature defining migration and forage habitat for marine resources. *Progress in Oceanography* 49(2001):469-483.

Polovina, J.J., P. Kleiber, and D.R. Kobayashi

1999. Application of TOPEX-POSEIDON satellite altimetry to simulate transport dynamics of larvae of spiny lobster, *Panulirus marginatus*, in the Northwestern Hawaiian Islands, 1993-1996. *Fishery Bulletin* 97:132-143.

Polovina, J.J., G.T. Mitchum, N.E. Graham, M.P. Craig, E.E. DeMartini, and E.N. Flint

1994. Physical and biological consequences of a climate event in the central North Pacific. *Fisheries Oceanography* 3:15-21.

Purcell, J.E., and M.N. Arai

2001. Interactions of pelagic cnidarians and ctenophores with fishes: A review. *Hydrobiologia* 155:27-44.

Randall, J.E.

1961. A contribution to the biology of the convict surgeonfish of the Hawaiian Islands, *Acanthurus triostegus sandvicensis*. *Pacific Science* 15:215-272.

Reese, E.S.
    1968. Annual breeding seasons of three sympatric species of tropical intertidal hermit crabs, with a discussion of factors controlling breeding. *Journal of Experimental Marine Biology and Ecology* 2:308-318.

Robertson, D.R.
    2001. Population maintenance among tropical reef fishes: Inferences from small-island endemics. *Proceedings of the National Academy of Science*, USA 98:5667-5670.

Seki, M.P., J.J. Polovina, R.E. Brainard, R.R. Bidigare, C.L. Leonard, and D.G. Foley
    2001. Biological enhancement at cyclonic eddies tracked with GOES thermal imagery in Hawaiian waters. *Geophys. Res. Letters*. 28(8):1583-1586.

Seki, M.P., J.J. Polovina, D.R. Kobayashi, and G.T. Mitchum
    2002. An oceanographic characterization of swordfish (*Xiphias gladius*) longline fishing grounds in the springtime subtropical North Pacific. *Fisheries Oceanography* 11(5):251-266.

Siegel, D.A., B.P. Kinlan, B. Gaylord, and S.D. Gaines
    2003. Lagrangian descriptions of marine larval dispersion. *Marine Ecology Progress Series* 260:83-96.

Sponaugle, S., R.K. Cowen, A. Shanks, S.G. Morgan, J.M. Leis, J. Pineda, G.W. Boehlert, M.J. Kingsford, K. Lindeman, C. Grimes, and J.L. Munro
    2002. Predicting self-recruitment in marine populations: Biophysical correlates. *Bulletin of Marine Science* 70(1, Supplement):341-375.

Sponaugle S., and D.R. Pinkard
    2004. Impact of variable pelagic environments on natural larval growth and recruitment of the reef fish *Thalassoma bifasciatum. Journal of Fish Biology* 64(1):34-54.

Swearer S.E., J.E. Caselle, D.W. Lea, and R.R. Warner
    1999. Larval retention and recruitment in an island population of a coral-reef fish. *Nature* 402:799–802.

Thresher, R.E.
    1984. *Reproduction in Reef Fishes*. TFH Publications, Inc. Ltd., Neptune City, NJ, USA. 399 pp.

Tolimieri, N., O. Haine, A. Jeffs, R. McCauley, and J. Montgomery
    2004. Directional orientation of pomacentrid larvae to ambient reef sound. *Coral Reefs* 23:184-191.

Victor, B.
    1987. Growth, dispersal, and identification of planktonic labrid and pomacentrid reef-fish larvae in the eastern Pacific Ocean. *Marine Biology* 95:145-152.

Walsh, W.J.
    1987. Patterns of recruitment and spawning in Hawaiian reef fishes. *Environmental Biology of Fishes* 18(4):257-276.

Zaret, T.M.
    1980. *Predation and Freshwater Communities*. Yale University Press, New Haven CT, USA. 187 pp.